ON DEVELOPMENT OF EARLY STAGES OF UROSALPINX CINEREA (SAY) AT CONSTANT TEMPERATURES AND THEIR TOLERANCE TO LOW TEMPERATURES

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One of the most destructive predators of young oysters in Long Island Sound is the oyster drill, *Urosalpinx cinerea* (Say). However, our knowledge of its early development and the tolerance of its egg cases to winter temperatures, when deposited late in the season, remains incomplete. Carriker's (1955) comprehensive review of the literature on oyster drills clearly shows that most workers, while mentioning the time needed for ova to develop into young conchs, neglect to give the temperature ranges at which development occurs. Among the few who offer information on this subject, Haskin (1935) states that within the temperature range of 23.3° to 29.1° C., 18 to 25 days are needed for the first protoconch to hatch. Federighi (1931) reports that within a range of 18.0° to 32.0° C., it takes approximately 40 days to complete the development. Stauber's field data (Carriker, 1955) indicate that within the temperature range of 15.0° to 25.0° C., from 45 to 78 days are required for drill eggs to develop. Cole (1942) reports 27 to 32 days at 22.6° C., and 44 to 55 days at 18.3° C.

As can be seen from the above references, the information is insufficient to form precise conclusions. We, therefore, devised experiments to determine more accurately the rate of early development of drills at several constant temperatures, which may be encountered within the temperature range of Long Island Sound or adjacent waters.

It was also considered of theoretical interest and practical importance to learn the fate of the eggs deposited so late in the fall that they cannot complete development. Such egg cases, collected during the winter from subtidal and intertidal zones, frequently contain live ova and veligers. Yet, no systematic observations on whether these eggs and embryos can survive the winter and be released in the spring have ever been made. If these embryos could develop, they would have an early start, thus adding to the destructive potential of the next year-class of drills.

Methods

Egg cases were obtained from drills maintained in the laboratory at 20.0° C. Preliminary experiments were made with egg cases scraped from the shells of the oysters used to feed the drills and from the glass sides of the aquarium. They were examined under a dissecting microscope and only those that had non-segmented ova, a soft pliable outer membrane, and a translucent bluish-white appearance were selected. It was estimated that such egg cases had been deposited within three days. Later, clusters of young oysters were placed in the aquarium overnight, and the egg cases deposited on them were used in the experiments. Thus, the age of these egg cases was known to be not more than 16 hours.

To determine the rate of development of ova at different constant temperatures, 20 egg cases were placed in perforated, transparent, plastic containers weighted with lead, which were then put in trays. Each tray was supplied with a constant flow of sea water at a salinity of about 25‰, and the temperature of the water was maintained at 7.5°, 10.0°, 15.0°, 20.0°, 25.0° and 30.0° C., controlled to within ± 1.0° C. (Loosanoff, 1949).

In addition to conducting experiments at the above constant temperatures, egg cases were also kept at chilling winter temperatures just above freezing, and others were exposed to sub-freezing temperatures in and out of sea water. For observations on the effects of the chilling temperature, 26 egg cases, dredged from New Haven Harbor on December 5, 1955, were suspended in outdoor tidal tanks and systematically examined until March 22, 1956. Egg cases were also taken in winter from an aquarium kept at 20.0° C. and gradually conditioned to the Harbor water temperature which, at that time, was approximately 1.3° C. On January 7, 1956, they were placed in the Harbor and kept there until July 20, 1956.

To expose the egg cases to sub-freezing temperatures, they were placed in the freezing compartment of a refrigerator. In the first experiment the temperature of the compartment was − 12.0° C. (± 1.0° C.), and in the second, − 16.0° C. (± 1.0° C.). In each experiment the egg cases, with ova and veligers, were preconditioned in sea water to 3.0° C. Altogether nine plastic boxes, each containing 20 egg cases, were used. Six containers were without water and three contained 100 ml. of sea water each. One container without water was removed at the end of the first half hour and the others at half-hour intervals thereafter, up to three hours. The first group of egg cases kept in sea water was removed after one hour of exposure and the others at hourly intervals. In later, similar experiments, the egg cases were left at both temperatures for two, four and six hours.

Development at Six Constant Temperatures

We determined the number of days required at different temperatures for development of ova (Fig. 1) to the following embryological stages: early larvae (Fig. 2), shelled veliger (Fig. 3), and protoconchs (Fig. 4). The time needed to reach the early veliger stage decreased with increases in temperature from 10.0° to 30.0° C. (Table I). The groups kept at 30.0° and 25.0° C. attained the shelled veliger stage between the fourth and seventh days. However, it required eight additional days for those kept at 20.0° C. to reach the same stage, and even longer for those at 15.0° and 10.0° C.

In spite of the longer time required for ova at 20.0° C. to develop to the shelled veliger stage, they had reached the protoconch stage by the 22nd day, the same as the groups kept at 25.0° and 30.0° C. Nevertheless, the egg cases kept at 30.0° and 25.0° C. started releasing young conchs on the 22nd day, and continued for 16 days for both temperature groups. None of those kept at 20.0° C. were released until the 30th day, and those kept at 15.0° C. were not released until the 56th day. Thus, while there was only eight days' difference in the time required to reach the protoconch stage between the egg cases kept at 20.0° C. and those at 15.0° C., there was 26 days' difference in the time of release of the first young conchs. Moreover, at 20.0° C. the period between the first conch released and the last was only 13 days, while for the 15.0° C. group 22 days were needed.

FIGURE 1. Egg case of *U. cinerea* with five ova. × 10.

At 10.0° C. the ova required 66 days to reach the early veliger stage, and 84 days before the shelled veligers appeared. At 7.5° C. no development occurred during the 54 days. At the end of those periods both the 10.0° C. and 7.5° C. groups were placed in water of 20.0° C. to determine whether they would develop under the new temperature condition, regardless of their previous treatment. Only 65 per cent of the egg cases kept originally at 10.0° C. produced conchs, while no development occurred in the former group at 7.5° C. Since the egg cases at 7.5° C. were apparently adversely affected before being placed at 20.0° C., it may be inferred that temperatures at 7.5° C. and lower not only arrested development, but killed the eggs after a prolonged period of exposure.

Our results indicated that the optimum temperature for drill development was

TABLE I

Number of days for ova to develop to various stages at constant temperatures and the percentage of egg cases producing young conchs

Stage of development	Temperatures					
	7.5° C.	10.0° C.	15.0° C.	20.0° C.	25.0° C.	30.0° C.
Early veliger	54*	66	10	7	4	2
Shelled veliger	—	84**	25	15	7	7
Protoconch	—	—	30	22	22	22
Release of young conchs	—	—	56–78	30–43	22–38	22–38
Percentage of egg cases producing young conchs	0%	65%	90%	100%	95%	90%

* No development.
** Placed in water of 20.0° C.

FIGURE 2. Egg case, with outer membrane removed, containing early motile larvae just before a true velum is developed. Larvae at this stage have a gut and can feed on particulate matter by means of currents created by the cilia. × 10.

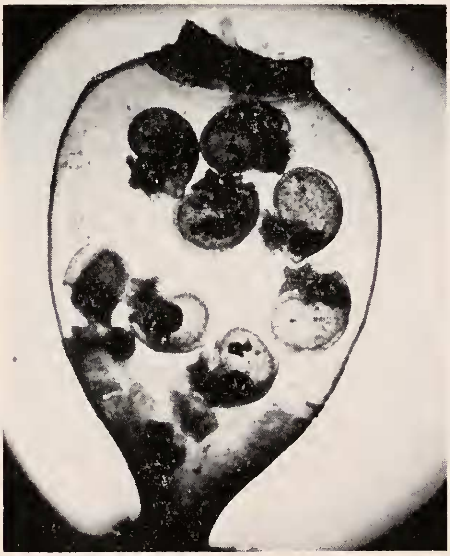

FIGURE 3. Egg case, with outer membrane removed, containing veliger larvae, with foot and velum present, after torsion has occurred. The shell has begun to form along the outer edge of the mantle. × 10.

about 20.0° C. (Table I). However, since the rate of development was faster at 25.0° C. and the difference in the percentage survival of egg cases producing young conchs between 20.0° C. and 25.0° C. was small, it was considered possible that the optimum was above 20.0° C. Therefore, a second experiment was conducted at 20.0° C. and 25.0° C., using 20 egg cases in each temperature group, and the percentage survival of ova determined. At 20.0° C., 139 out of 176 ova, or 78.9 per cent, developed to the protoconch stage, as compared to 96 out of 168 ova, or 56.8 per cent development, at 25.0° C. Thus, although the rate of development was faster at 25.0° C., the optimum temperature, from the standpoint of successful development to the young conch stage, appeared to be about 20.0° C. Moreover, at 20.0° C. the period for protoconch release was shorter than at any other temperature.

FIGURE 4. Egg case, with outer membrane removed, containing three early protoconch larvae which show partial spiral development and pigmentation. Note also the two undeveloped ova in the same egg case. × 10.

Since the egg cases in the first experiment were deposited within a period of three days, their age alone could not account for the difference of 13 to 22 days between the release of the first and last young conch. The conclusion that slight differences in the age of the cases are not responsible for pronounced differences in the time needed for release of young conchs of the same groups is further substantiated by our second experiment at 15.0° C. in which egg cases collected within a 16-hour period started releasing young conchs at 62 days and continued to do so for 19 days.

TOLERANCE TO LOW TEMPERATURES

To study the tolerance of egg cases to winter temperatures when exposed at low tide and to simulate tide pool conditions, cases containing ova and veligers were placed in water and exposed to air at the same sub-freezing air temperatures.

Because oyster drills in the intertidal zone stay close to the low water level and deposit their egg cases there, the latter are seldom exposed to air for more than an hour or two. Nevertheless, even under these conditions all the eggs would die if exposed to air temperatures around − 15.0° C. However, if the time of exposure at this temperature is reduced to a half hour, approximately 40 per cent may survive. At temperatures around − 12.0° C., five per cent could survive after two hours of exposure.

The survival was greater when the egg cases were protected by water (Table II). At exposure periods of two hours at air temperatures around − 12.0° and − 15.0° C., about 95 per cent of the eggs survived. The chance of survival of eggs in frozen tide pools would be much greater than in air, not only because of the

TABLE II

Survival of ova and veligers in egg cases of U. cinerea (a) submerged in sea water, and (b) when exposed in air, subjected to two sub-freezing temperatures. Survival is expressed in percentage of egg cases in which shelled veligers developed after returned to 20.0° C. sea water

Air temperature −12.0° C. (±1.0° C.)			Air temperature −16.0° C. (±1.0° C.)		
Length of exposure	Temperature at end of exposure (°C.)	Survival (%)	Length of exposure	Temperature at end of exposure (°C.)	Survival (%)
(a) submerged in sea water					
1 Hr.	− 1.8	100	1 Hr.	− 5.0	90
2 Hrs.	− 2.8	95	2 Hrs.	− 5.0	95
3 Hrs.	− 3.0	95	3 Hrs.	− 8.1	25
4 Hrs.	− 3.5	95	4 Hrs.	−12.0	25
6 Hrs.	− 7.5	85	6 Hrs.	−16.0	0
(b) exposed in air					
½ Hr.	−11.0	75	½ Hr.	−15.0	40
1 Hr.	−11.0	20	1 Hr.	−15.0	0
1½ Hrs.	−11.2	5	1½ Hrs.	−15.0	0
2 Hrs.	−11.5	5	2 Hrs.	−15.3	0
2½ Hrs.	−11.8	0	2½ Hrs.	−16.2	0
3 Hrs.	−12.4	0	3 Hrs.	−16.0	0

warmer temperatures of the water, but also because desiccation of the egg cases is inhibited. Usually when drill cases were exposed to the sub-freezing air temperatures they were desiccated to such an extent that their walls collapsed. In general, experiments showed that the percentage survival in both air and water decreased with increases in time of exposure and with decreases in temperature (Table II).

The resistance of eggs and embryos to low temperature was tested under more natural conditions when, on December 5, 1955, 26 egg cases, 11 of which contained ova to segmented stages and 15 contained veligers and shelled veligers, were dredged from New Haven Harbor. The bottom temperature was 7.1° C. and the veligers were observed revolving within their capsule. These cases were placed in tidal tanks in water of 7.5° C. on December 6, 1955, and the veligers were still motile on February 16, 1956, 63 days later. The average water temperature during this period was 2.3° C. with a range from − 0.1° to 7.5° C. By March 22, however, the ova and segmented stages within the cases were disintegrated and the veligers were dead.

To supplement these observations 120 egg cases collected from the laboratory aquaria were conditioned gradually to the outdoor water temperature of 1.3° C. and placed in the Harbor on January 7, 1956. These egg cases were kept until July 20, 1956, but showed no evidence of development.

Discussion

The incubation times found in our experiments are in general agreement with the data of other authors. Thus, Haskin's (1935) report of 18 to 25 days as the time for the first young conchs to hatch at 23.3° to 29.1° C. agrees with our 22-day period at 25.0° C. Cole's (1942) findings of 27 to 32 days at 22.6° C. and 44 to 50 days at 18.3° C. for drills are again in agreement with our observations. If we interpolate our data, we obtain 30 to 38 days at 22.5° C. and 43 to 56 days at 17.5° C.

Compared to our results, Cole (1942) found that the surprisingly short period of only five days was required for all the young conchs to be released at 22.6° C. and only six days at 18.3° C. Cole does not give the number of egg cases used in this experiment and the short period he records may be the result of having very few egg cases, since we found considerable variation between egg cases at any one temperature.

Pope (Carriker, 1955) found that the period for protoconch release from an egg case or group of egg cases, which we assume were deposited at the same time and kept under identical conditions, extended from four to 38 days. He attributes this to an uneven development of the embryos, but we found the embryonic development within a single egg case to be generally uniform, except for malformed embryos and undeveloped ova. By the time of release, some of these are partly eaten by the normally developing drills or remain undeveloped to such an extent that they never emerge (Fig. 4). Considerable variation in the period of incubation, however, does occur between the egg cases deposited within a 16-hour period.

We observed that the greatest variation in hatching time between egg cases occurs after the protoconch stage, which may not be caused entirely by an uneven development of the embryos. Some protoconchs remain in their cases longer than others, which may be due to a variation in some mechanism releasing the egg case operculum. Variations in hatching may also be caused by the physical obstruction of the operculum opening which a protoconch may find too small. On one occasion we saw a young drill, emerging from a case, become entrapped in the operculum opening and block the passage for the remaining protoconchs for eight days.

Our experiments showed that although egg cases can withstand sub-freezing water temperatures for short periods, they cannot survive prolonged periods of chilling. At first it appears to be more drastic to subject the egg cases to sub-freezing temperatures rather than to temperatures above freezing but if, for example, the permeability of the egg cases is affected, the osmotic malfunction progresses at a faster rate at chilling temperatures than at sub-freezing temperatures (Luyet and Gehenio, 1940). Chilling temperatures, as these authors point out, become lethal to protoplasm only after long periods. This may explain the survival of the egg cases which we kept in the tidal tanks for a period of 63 days and also the presence of egg cases observed by other workers during the winter months (Carriker, 1955).

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Summary

1. The rate of ova development increases directly with the increase in temperature from 15.0° to 25.0° C. No increase in the rate of ova development was observed above 25.0° C.

2. Optimum temperature for ova development of *U. cinerea* of Long Island Sound appears to be 20.0° C., or between 20.0° and 25.0° C.

3. Egg cases of *U. cinerea* kept in sea water can withstand sub-freezing temperatures for longer periods than egg cases exposed to sub-freezing air temperatures.

4. In sub-freezing temperatures, the percentage mortality increases with the period of exposure and with a decrease in temperature.

5. Egg cases kept at 10.0° C. for as long as 84 days showed partial development and were capable of producing normal protoconchs when returned to 20.0° C.; whereas, egg cases kept at 7.5° C. for 54 days were not viable.

6. Our experiments and observations suggest that egg cases remaining through the winter in Long Island Sound will not contain viable ova in the spring.

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